A phylogenetic approach to disentangling the role of competition and habitat filtering in community assembly in Neotropical forest birds

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Diciembre, 2008
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Abstract
Novel methods allow making inferences about the processes involved in the coexistence of species and community assembly using predicted patterns of phylogenetic relationships and character distribution and evolution. Under phylogenetic niche conservatism, assemblages should shift from phylogenetic overdispersion to phylogenetic clustering with increasing geographic scale. By using assemblage species lists, trait information and a molecular phylogeny, we attempt to explain the high diversity patterns of typical antbirds in neotropical assemblages. We find a shift from phylogenetic clustering to overdispersion as the geographical scale is increased, opposite to the predictions. However, trait evolution among typical antbirds and distribution within assemblages allow us to conclude that antbirds do not expose phylogenetic niche conservatism and that habitat filtering is the predominant force involved in regional community assembly. Alternatively, competitive interactions may not play an important role at local scales, providing a plausible explanation to the high antbird diversity at specific locations in Amazonian forests.

Introduction
Studying the phylogenetic structure of assemblages allows bridging ecology and evolutionary biology to further our understanding of the processes that prevent or allow
species coexistence (Webb et al. 2000; Webb et al. 2002; Cavender-Bares et al. 2004; Cavender-Bares et al. 2006; Johnson & Stinchcombe 2007). Assuming that closely related species have similar ecological niches (Peterson et al. 1999; Wiens & Graham 2005), competition and limiting similarity (MacArthur & Levins, 1967) could result in assemblages whose constituent species are less related than expected by chance (i.e. phylogenetic overdispersion). Alternatively, habitat filtering might force species that are more related than expected by chance to coexist (i.e. phylogenetic clustering), because such species are thought to be more likely to possess traits that allow them to establish populations in particular environments (Webb et al. 2000; Webb et al. 2002). However, competition and habitat filtering are not mutually exclusive forces, and may act in concert to influence assemblage structure; in fact, these forces might even mask each other's effect, producing assemblages in which species are not more closely or distantly related than expected by chance (Helmus et al. 2007).

Furthermore, it has been hypothesized that patterns of phylogenetic structure of assemblages are influenced by geographic scale, because the processes involved in community assembly may act in a scale-dependent fashion (Cavender-Bares et al. 2006; Swenson et al. 2007; Emerson & Gillespie 2008). Interspecific competitive interactions among species are thought to structure assemblages predominantly at local scales due to low habitat heterogeneity, and thus, few opportunities for niche partitioning (MacArthur & Levins 1967; Keddy & Weiher 1999). In contrast, at large spatial scales, habitat heterogeneity should weaken interspecific competitive interactions, making the species' ability to overcome habitat filters the predominant limitation for species coexistence (Weiher & Keddy 1995; Keddy & Weiher, 1999).
Consequently, if closely related species are more ecologically similar than distant relatives (Peterson et al. 1999; Wiens & Graham 2005), the patterns of phylogenetic structure should vary across spatial scales: local assemblages should show phylogenetic overdispersion as a result of competitive exclusion among close relatives, whereas assemblages at larger scales should show increased phylogenetic clustering resulting from the effects of habitat filtering.

Several recent studies have made inferences about the role of competitive interactions and habitat filtering on community assembly based on their phylogenetic structure. For instance, studies on local mammal assemblages have revealed that these are often composed by species that are less related than expected by chance, which seemingly supports the idea that competitive interactions influence community assembly at local scales (Cardillo et al. 2008; Cooper et al. 2008). Likewise, phylogenetic overdispersion in plant assemblages has been interpreted as a probable result of competition among species (Bryant et al. 2008). These studies did not evaluate the phenotypic structure of assemblages and did not explicitly test hypotheses of ecological trait evolution, so their conclusions rely on the assumption that phenotypic overdispersion allows coexistence, and that co-occurrence of distant relatives is a reflection of phylogenetic niche conservatism.

Combining analyses of phylogenetic structure with analyses of the distribution and evolution of ecologically relevant traits among species within and among assemblages, allows a more detailed understanding of assembly processes. Additionally, it avoids the need to assume that species exhibit phylogenetic niche conservatism, an assumption that is not always met (Losos 2008). Several studies suggest that local tree
Assemblages tend to be phylogenetically overdispersed and regional ones tend to be phylogenetically clustered (Cavender-Bares et al. 2004; Cavender-Bares et al. 2006; Swenson et al. 2006; Swenson et al. 2007). As with the mammal and plant assemblages described above (Bryant et al. 2008; Cardillo et al. 2008; Cooper et al. 2008), these patterns might be interpreted to suggest that niche conservatism prevents close relatives from coexisting at local scales as a result of competition and allows them to coexist at regional scales as a result of habitat filtering. This was further supported by analyses of phenotypic structure and trait evolution, which showed that species co-occurring locally often exhibit traits that are less similar than expected by chance; because these traits are often phylogenetically conserved, ecological similarity of closely related taxa likely prevents their local coexistence as a result of competition (Cavender-Bares et al. 2004; Cavender-Bares et al. 2006; Swenson et al. 2007).

Despite the important contribution of ornithological studies to the development of classic ideas about community assembly and structure (MacArthur 1958; Diamond 1975; Cody 1975), little research using phylogenetic approaches has been conducted on bird community ecology. The only published study assessing phylogenetic structure of assemblages we are aware of, found that wood warbler species (Parulidae) that coexist locally in areas of North America are less related than expected by chance (Lovette & Hochachka 2006). This suggests that interactions among closely related species sharing ecological traits do not allow coexistence, whereas coexistence of distantly related species is mediated by ecological and behavioral divergence. However, these authors did not explicitly evaluate the evolution of traits of ecological importance in a phylogenetic framework.
The high species richness of antbirds (Aves, Thamnophilidae) at many Neotropical sites, especially Amazonian forests where as many as 45 species may coexist (Ridgley & Tudor 1994), represents a great challenge for explaining diversity and coexistence patterns in birds. This exclusively Neotropical radiation comprises nearly 220 species occurring from central Mexico to northern Argentina, and ranging from the lowlands up to c. 2600 m (Zimmer & Isler 2003). They exhibit considerable variation in some phenotypic and ecological traits that presumably facilitate species’ coexistence. For instance, co-occurring antbirds vary substantially in body size (Robinson & Terborgh 1995), vocalizations (Isler et al. 1998; Seddon 2005), plumage patterns and coloration (Irestedt et al. 2004), foraging strata (Parker et al. 1996), microhabitat use (Isler et al. 2001; Isler et al. 2002), and foraging behavior, including extreme cases of specialization (e.g. finding insects only on dead leaves or by following ant swarms; Munn & Terborgh 1979, Remsen & Parker 1984, Kratter 1997, Rosenberg 1997). The presumed role of these phenotypic and ecological differences on explaining diversity patterns at different geographic scales remains to be tested. Also, the availability of a robust and comprehensive species-level phylogeny for the family (Brumfield et al. 2007; R.T. Brumfield et al. unpubl. data), makes antbirds an ideal model to conduct studies on phylogenetic structure and character evolution to better understand community assembly.

Here, we integrate information on phylogenetic relationships, phenotypic variation, and species composition of antbird assemblages at different spatial scales to provide insights about the processes governing community assembly in antbirds. Specifically, we use analyses of phylogenetic structure to test the hypotheses that competitive
interactions should shape species assemblages at local scales, whereas habitat filtering should predominate at regional scales. These hypotheses predict that, under phylogenetic niche conservatism, local assemblages should exhibit phylogenetic overdispersion and regional assemblages should exhibit phylogenetic clustering. However, we do not simply assume that ecological niches are conserved. Instead, we follow recent suggestions (Losos 2008) and explicitly test for phylogenetic niche conservatism using comparative methods evaluating the evolution of different sets of ecologically relevant traits, and combine this with analyses of the phenotypic structure of assemblages. Our results allow a more comprehensive understanding of the processes that govern the assembly of communities at local and regional scales, and provide a new perspective towards the understanding of the exceptionally high diversity of Neotropical avian assemblages.

Methods

Phylogenetic analysis
We used DNA sequence data from one nuclear (β-Fibrinogen Intron 5) and three mitochondrial loci (ND2, ND3, and Cytochrome B) to reconstruct relationships among 151 species of antbirds. Some of these sequence data have been published (Brumfield & Edwards, 2007; Brumfield et al. 2007), and the rest were provided by R. Brumfield and colleagues, who will publish a complete phylogeny of the family separately. We performed a maximum-likelihood analysis using the GTR+I+G model of nucleotide substitution as implemented in the program RAxML (Stamatakis, 2006) available on the CIPRES portal (www.phylo.org). We also used the program BEAST (Drummond & Rambaut, 2007) to estimate phylogeny and branch lengths simultaneously in a
Bayesian framework under a relaxed molecular clock approach (Drummond et al. 2006). Results obtained with both methods were similar; therefore, here we present analyses based on the maximum-likelihood tree obtained using RAxML.

**Phylogenetic structure of assemblages**

*Definition of assemblages and species pools*

We evaluated patterns of phylogenetic structure of antbird assemblages at three different spatial scales: highly local, intermediate, and regional. Based on the presumed relative importance of competitive interactions and habitat filtering at different geographical scales and assuming phylogenetic niche conservatism (Wiens & Graham, 2005), we expected a shift from phylogenetic overdispersion to phylogenetic clustering as the geographical scale is increased.

The highly local scale is represented by individual mixed-species flocks occurring at single localities. Mixed-species flocking is a common social system among Neotropical forest birds, in which at least 11 species of antbirds commonly participate (Munn 1985). These flocks are relatively persistent assemblages containing few individuals (pairs or small family groups) of up to ca. 25 species that move about together (Munn 1985; English 1998; Julien & Clobert 2000). This behavior is thought to be adaptive by increasing foraging efficiency and decreasing risk of predation, leading to increased survival (Munn 1985; English 1998; Julien & Clobert 2000). At this scale, opportunities for resource partitioning are expected to be limited; accordingly, null model analyses reveal that mixed-flock assembly appear to be strongly influenced by competitive interactions (Graves & Gotelli 1993). The data sets used at this scale correspond to lists of antbird species co-occurring in 25 canopy and seven understory mixed-flocks at
Cocha Cashu Biological Station, SW Peru (Munn 1985) and in five understory flocks at forests near Manaos, Brazil (Develey & Stouffer 2001).

At the intermediate scale, we defined assemblages as the group of species coexisting in thoroughly sampled 100-ha plots in forested habitats. Plots of this size have been surveyed for bird communities in different areas of the Neotropics over the last two decades, and it has been suggested that 100-ha represent the smallest plot size that adequately reflects avian $\alpha$-diversity in the region (Terborgh et al. 1990; Robinson et al. 2000). Analyses at this scale are based on data from (1) Western Amazonia: three plots from Ecuador (English 1998; Blake 2007) and one from Peru (Terborgh et al. 1990); (2) Central Amazonia: six plots from near Manaos (TEAM Project unpubl. data, M. Cohn-Haft & P. Stouffer unpubl. data) and two from the Rio Tapajos, Brazil (Wunderle et al. 2006); (3) Eastern Amazonia: one plot from French Guiana (Thiollay 1994); and (4) Central America: one plot from Panama (Robinson 2000), four from Costa Rica (TEAM project, unpubl. data), and one from Honduras (D. Anderson, unpubl. data; Fig. 1).

Finally, the regional scale comprises assemblages consisting of the group of species known to occur within different ecoregions in Amazonia. Ecoregions refer to large areas containing a geographically distinct assemblage of natural communities, and are defined based on broad-scale vegetation maps, in combination with floristic and zoogeographic regions (Olson et al. 2001; Olson & Dinerstein 2002). We focused on the Amazonian portion of the Tropical and Subtropical Moist Broadleaf Forests Biome, because this was the area for which we had the most complete information on antbird assemblages and this is where the family reaches its highest diversity. The list of antbird species occurring in each Amazonian ecoregion was extracted from an updated
distributional database (see Isler 1997) by overlapping shape files for each ecoregion (http://www.worldwildlife.org/science/data/item6373.html) onto the distributional data using the program ArcGIS v 9.3.

To assess the phylogenetic structure of antbird assemblages at each scale, we needed to establish a species pool, which we defined as the list of species that could potentially occur in each assemblage. The species pool at the highly local scale included all the antbird species that are known to join mixed-species flocks at each locality where flocks were censused. At the intermediate scale, the species pool was the species list for the ecoregion in which each plot was embedded. At the regional scale, the pool includes all the species coexisting within the area of endemism (i.e., an area in which there is congruence among the geographical ranges of multiple taxa, which indicates a shared history of isolation and diversification; Cracraft 1985) where the ecoregion is located.

Quantifying the phylogenetic structure of assemblages

We used the program Phylocom version 4.0.1b (Webb et al. 2008) to calculate two basic metrics of phylogenetic structure for each assemblage. The Mean Pairwise Phylogenetic Distance (MPD) is the mean phylogenetic distance observed between each pair of species present in the assemblage; and the Mean Minimum Phylogenetic Distance (MMPD) is the mean phylogenetic distance between each species in the assemblage and its closest co-occurring relative (Webb et al. 2002; Swenson et al. 2006). Phylocom calculates null MPD and MMPD based on 1000 communities assembled randomly from a pool of species that can potentially coexist. Using the observed and null MPD and MMPD, and their standard deviations, two indices of relatedness at the assemblage level are calculated as follows:
Net Relatedness Index (NRI) = \(-1 \times (MPD - \text{mdMPD}) / \text{sdrndMPD}\)

Nearest Taxon Index (NTI) = \(-1 \times (MMPD - \text{mdMMPD}) / \text{sdrndMMPD}\)

In these equations, \(\text{mdMPD}\) and \(\text{mdMMPD}\) are the mean values of MPD and MMPD obtained from the 1000 communities assembled randomly and \(\text{sdrndMPD}\) and \(\text{sdrndMMPD}\) are their standard deviations. Values of NTI or NRI greater than zero indicate phylogenetic clustering, and values lower than zero indicate phylogenetic overdispersion (Webb et al. 2002; Swenson et al. 2006).

The results of the NTI and NRI indices may indicate whether species are more closely or distantly related than expected by chance in an assemblage or that the prevalence of closely or distantly related species is higher than expected by chance. This might be particularly problematic if we are trying to explain patterns of coexistence and not of prevalence. In order to solve this, we used the treewise PSV index (Helmus et al. 2007), which is not sensible to species prevalences, and compared it to the results obtained with the NRI. Results obtained with both methods were similar; therefore, here we present analyses based on the NRI and NTI.

**Analyses of Phenotypic Structure of Assemblages and Trait Evolution**

*Selection of traits and data collection*

We explicitly tested for phylogenetic niche conservatism evaluated because assuming this exists is not always justified (Losos et al. 2008; Warren et al. 2008). Also, assessments of the degree of trait conservativeness, when coupled with analyses of phylogenetic and phenotypic structure, provide insights on the processes involved in community assembly (Webb et al. 2002, Cavender-Bares et al. 2004). Accordingly, we also characterized the phenotypic structure of assemblages by determining if traits of
co-occurring species within an assemblage were more or less similar than expected by chance. Analyses of trait evolution and phenotypic structure were based on a selection of a total of 51 traits of ecological relevance (Table 1). This selection includes what we categorize as both α and β traits, a designation that is analogous to local (α) and regional (β) measures of biodiversity (Swenson et al. 2006; Ackerly & Cornwell 2007).

Alpha (α) traits are the ones that presumably allow species coexistence at local scales (i.e. traits allowing for niche partitioning); these traits should show variation among species locally. Beta (β) traits are those that presumably allow overcoming habitat filters at regional scales and should vary among regional assemblages but be similar within assemblages.

Due to the relationship between morphological and ecological variation that may be important for resource partitioning locally (e.g. Miles & Ricklefs 1984), we treated morphological variation as an α trait. To characterize morphological variation across the family Thamnophilidae, one of us (G.A.B.) took ten standard morphological measurements (Table 1) on museum specimens, using one specimen per each of a total of 140 species available at the Louisiana State University Museum of Natural Science (LSUMZ), the National Museum of Natural History (NMNH), and the American Museum of Natural History (AMNH). Another character that we considered to be involved with local assemblage structuring (i.e. an α trait) is foraging stratum, which has been shown to be an important axis of ecological differentiation in forest birds (Marra & Remsen 1997). We considered the foraging stratum used by each species of Thamnophilid assigning a value ranging from one to five to each of the categories proposed by Parker et al. (1996), with one representing terrestrial species and five
canopy species. Species that forage at two different strata received the corresponding intermediate value. Finally, considering that species might compete for acoustic space (Ryan & Brenowitz 1985), and that Thamnophilid songs show evolutionary divergence in response to interspecific interactions between sympatric close relatives (Seddon 2005), vocal traits were also treated as $\alpha$ traits. To characterize vocal variation, we measured 18 vocal traits that are thought to be important for interspecific acoustic recognition (see Seddon 2005) and species delimitation in antbirds (see Isler et al. 1998), which are related to frequency (10) and temporal aspects (8) of songs (Table 1) on spectrograms generated for a single loudsong recording of each Thamnophilid species obtained from Isler & Whitney (2002). Although we are aware that intraspecific variation in morphology and vocalizations exists and that this may introduce undesired errors respective to the distance of each individual to the species mean, our analyses assume that intraspecific variation is substantially smaller than interspecific variation and that one individual is sufficient to provide an approximate species value for the purposes of our analyses. In addition, this assumption was necessary to allow us to conduct a coarse characterization of a large number of species for multiple traits across the entire family.

The $\beta$ traits used in our analyses correspond to climatic and topographic variables that characterize areas where species are known to occur, i.e. a multivariate description of the species' realized Hutchinsonian niches (Keamy 2006). These traits include 19 climatic variables related to temperature and precipitation obtained from WorldClim (Hijmans et al. 2005; layers at 1 Km$^2$ resolution); and three topographic variables: elevation, obtained from WorldClim, and slope and aspect calculated in ArcGIS (version
9.0) based on the elevation layer. To obtain the macroecological data for each species, we used ArcGIS to extract the value of each variable from occurrence localities available in Isler’s (1997) distributional database for antbirds, and calculated an average value per variable per species.

We reduced each multivariate data set (i.e. morphology, vocalizations, macroecological variables) to an uncorrelated set of variables using Principal Component Analyses (Table 1). We then used the factor scores obtained following varimax rotation as independent variables for subsequent analyses of phenotypic structure and trait evolution.

We examined the phenotypic structure and the degree of phylogenetic conservativeness for different sets of characters at different scales. At the highly local and intermediate scales we considered only $\alpha$ traits, whereas at the regional scale we considered only $\beta$ traits.

Phenotypic structure of assemblages
In order to determine if traits of species coexisting in the different assemblages are more or less similar than expected by chance, we used Mantel tests to correlate matrices of species co-occurrence distances with matrices of trait distances between species (Cavender-Bares et al. 2006). Co-occurrence distance matrices were calculated using the species.dist function in the package Picante for R (developed by S. Kembel et al. 2008) using Schoener’s index of co-occurrence (Schoener 1970). Trait Euclidean distance matrix was calculated using the dist function in R (R Development Core Team 2005). We examined significance of correlations using two-tailed tests based on null
distributions based on 1000 randomizations of the co-occurrence matrices. Mantel tests were performed using the Ecodist package for R (Goslee & Urban 2007).

In the Mantel analyses described above, a significant positive correlation indicates that species that co-occur are phenotypically less similar than expected by chance (phenotypic overdispersion), whereas a significant negative correlation indicates that coexisting species are more similar than expected by chance (phenotypic clustering). Observed matrices correlation coefficients lying on the first or last 25 quantiles of the 1000 randomizations were considered significant. Based on the expected roles of competition and habitat filtering at different scales, we expected $\alpha$ traits to show phenotypic overdispersion at the highly local and intermediate scales and $\beta$ traits to exhibit phenotypic clustering at regional scales.

**Analysis of trait evolution**

In order to assess whether different traits have been evolutionarily conserved or labile in antbirds, we conducted two separate tests using the multiPhylosignal function in Picante. First, we used a test for phylogenetic signal to determine whether closely related species are more or less similar than expected by chance, and then we quantified the phylogenetic signal of traits to evaluate if they are more conserved or labile than expected based on the branch lengths separating species in the phylogeny (i.e. under a Brownian motion model of evolution). Phylogenetic niche conservatism is assumed when closely related species are more similar than expected by chance and show more phylogenetic signal than expected under a Brownian motion model of evolution. In turn, the hypothesis of phylogenetic niche conservatism may be rejected
even if there is phylogenetic signal but such signal is weaker than expected under Brownian evolution.

The randomization test for phylogenetic signal (Blomberg *et al.* 2003) consists of calculating the variance of the independent contrasts of each trait across the antbird phylogeny and comparing the empirical value with a null distribution of the variance of trait's independent contrasts obtained based on 1000 randomizations of the traits among species. If observed traits show lower variance than the mean of the null distribution, then traits are said to exhibit phylogenetic signal (i.e. closely related species resemble each other more than expected by chance). If observed traits show higher variance than the null mean, traits are said to exhibit antisignal (i.e. closely related species are less similar than expected by chance). Observed trait variance lying on the first or last 25 quantiles of the 1000 randomizations was considered as significant phylogenetic signal or antisignal.

We used the K statistic (Blomberg *et al.* 2003) to quantify the strength of the phylogenetic signal obtained from the randomization test. This statistic measures the amount of phylogenetic signal exhibited by traits relative to the amount of phylogenetic signal expected for traits evolving under a Brownian motion model of evolution. Under such a model, the differences in traits between species are expected to be proportional to the branch lengths separating them on the phylogeny. If the observed K statistic is greater than one, then traits are said to be conserved because they evolve slower than expected under Brownian motion; if the observed K statistic value is lower than one, then traits are said to be labile because they evolve faster than expected under Brownian motion.
Results

Phylogenetic structure of assemblages
In contrast to our initial expectations, local antbird assemblages generally consist of species that are more closely related than expected by chance, whereas regional assemblages tend to consist of distant relatives. Specifically, based on the NTI, local understory mixed flock assemblages are phylogenetically clustered (Cocha Cashu NTI = 1.03 95% C.I. = 0.76-1.3; Manaos NTI = 1.62 95% C.I. = 1.4-1.84), whereas canopy mixed flocks do not show significant phylogenetic structure (Cocha Cashu NTI = 0.19, 95% C.I. = -0.08, 0.46). The intermediate scale 100-ha plots do not show significant phylogenetic structure (Western Amazonia NTI= 0.442 95% C.I. = -0.43, 1.31, Central Amazonia NTI =-0.311 95% CI = -0.891, 0.269, Central America NTI = -0.44, 95% CI = -1.35, 0.47, Eastern Amazonia, NTI = -1.282 p = 0.2). Finally, the regional-scale Amazonian ecorregions exhibit significant phylogenetic overdispersion (Ecorregions NTI = -1.37 95% CI = -1.7,-1.04; Fig. 2). The NRI generally showed the same patterns of phylogenetic structure as the NTI (Fig 2.).

Phenotypic structure of assemblages.
In general, species coexisting at local scales do not show phenotypic overdispersion as expected based on the hypothesis that coexistence would be facilitated by phenotypic differentiation at such scales. Specifically, \( \alpha \) trait values of species co-occurring in mixed-species flocks in Manaos and Canopy mixed-flocks at Cocha Cashu, are not more or less similar than expected by chance (Fig. 3; Table 2); likewise, understory mixed flocks in Cocha Cashu, tended to lack phenotypic structure except for tail size (i.e. PC3 of the morphological data set), which showed phenotypic overdispersion (Fig,3; Table 2). One-hundred ha plots showed random phenotypic structure for \( \alpha \).
traits, except for measurements of wing, tarsus, and hallux size (i.e. PC1 of the morphological data set), which showed phenotypic clustering in the Western Amazonian assemblages. Finally, as predicted by the hypothesis of habitat filtering, at the ecoregion scale, co-occurring species are more similar in β traits than expected by chance (phenotypic clustering; Fig. 3; Table 2).

**Trait Evolution**

In general, ecologically relevant traits tended to show significant phylogenetic signal in antbirds as indicated by the randomization test irrespective of whether they were considered α or β traits (Table 3). This means that closely related species are phenotypically and ecologically more similar than expected by chance. There were two sets of traits that did not conform to this pattern: a summary of temporal measurements of vocalizations (i.e. PC2 extracted from the vocal data set; Table 1) showed marginally significant phylogenetic antisignal (closely related species are less similar than expected by chance), and a composite variable related to aspect, slope, and temperature and precipitation in dry and warm periods (PC2 extracted from macroecological variables; see Table 1) showed no significant phylogenetic signal.

Despite exhibiting phylogenetic signal, traits tended to be evolutionarily labile because the resemblance between species is generally lower than expected under a Brownian motion model of evolution (i.e. most traits exhibited K statistics lower than 1; Fig. 3; Table 3). Only two sets of traits were relatively conserved (K > 1): a general measure of wing, tarsus and hallux size (i.e. morphology PC1), and foraging stratum (Fig. 3; Table 3). The combination of these results allowed us to reject the hypothesis of phylogenetic niche conservatism, because closely related species are generally not
more similar than expected under a Brownian motion model of evolution. Additionally, some traits showed at least marginally significant phylogenetic antisignal, an indication of lack of phylogenetic niche conservatism (see Losos 2008).

Discussion

Inferences about the role of competition and habitat filtering structuring assemblages

To our knowledge, this is the first study that combines analyses of phylogenetic and phenotypic structure of assemblages with explicit assessments of trait evolution in order to determine the forces involved in the process of community assembly in birds. Generally, our findings regarding the phylogenetic structure of assemblages appear seemingly opposite to those predicted based on the expected role of competitive interactions and habitat filtering in assembly processes at different scales. Assuming phylogenetic niche conservatism, the hypothesis that competition predominates at small scales and habitat filtering at larger scales predicts that antbird assemblages should shift from phylogenetic overdispersion at local scales to phylogenetic clustering at regional scales. In contrast, we found that the phylogenetic structure of antbird assemblages shifts from significant phylogenetic clustering at local scales (i.e. mixed-species flocks) to significant phylogenetic overdispersion at regional scales (i.e. Amazonian ecoregions), with no phylogenetic structure at intermediate geographical scales (i.e. 100-ha plots).

The apparent lack of congruence between our assessments of the phylogenetic structure of antbird assemblages and the predictions of our hypotheses can be partly reconciled considering the analyses of phenotypic structure and trait evolution. At the
regional scale, \( \beta \) traits do tend to be more similar among co-occurring species than expected by chance, as predicted by habitat filtering. However, regional assemblages actually consist of distant relatives, in contrast to the prediction that they should consist of close relatives assuming that close relatives are ecologically similar. This finding is, in fact, fully consistent with the hypothesis that habitat filtering is important for assembly at regional scales because our analyses reveal that antbirds generally do not exhibit phylogenetic niche conservatism: almost all traits appear to be evolutionary labile despite a general tendency for them to exhibit phylogenetic signal. Thus, distantly related species have often converged to similar \( \beta \) traits that likely allow their coexistence in particular environments at large spatial scales (Fig. 3). This might be the most striking result of our study. Although, it was not surprising that coexisting antbirds in ecoregions share similar \( \beta \) traits because intrinsically, ecoregions may not vary too much in their climatic conditions as they are defined by the congruence of floristic and zoogeographic regions. In this way, phenotypic clustering in antbird regional assemblages may be partly explained by the way ecoregions are defined. However, what is interesting here is the mechanism by which distantly related species of antbirds have converged to the same tolerances and preferences of climate driven by the lability of \( \beta \) traits that allow distant relatives to colonize the same ecoregion. It may result obvious the finding of phenotypic clustering at this scale, but it was a forced path to completely test for habitat filtering effects over antbird assemblages.

In contrast to our prediction based on the assumption of niche conservatism and the expected role of competition structuring local assemblages, at the most local scale, antbird assemblages are composed by closely related species. One might be able to
reconcile the observed pattern with the hypothesis of competition considering that the lability exhibited by $\alpha$ traits (Table 3) may allow closely related species to co-exist because they are likely to differ ecologically. However, $\alpha$ traits at this scale did not exhibit significant phenotypic structure (Fig. 3). This might suggest that species that coexist at this scale do not compete as strongly as expected. Alternatively, competition might still be important for assembly at this scale, but the traits allowing for niche differentiation and coexistence might not be the ones we evaluated. It is also possible that not all $\alpha$ traits selected to test for competition show high divergence in sympatry, and the reduction of variables to principal components in our analyses reduces the importance of a few traits that might be influenced by competition, increasing type II error. However, we did not analyze each trait separately because many of these traits were correlated and also because increasing the number of variables would result in a high number of tests, which may increase the probability of type I error. In addition, competitive interactions among closely related antbirds might not be reflected in presence/absence patterns, but rather in terms of how abundant species are within assemblages (Anderson et al. 2004; Kelly et al. 2008). For example, competitive interactions between closely related yeast species are presumably stronger than those between distantly related species, an effect that is evident from comparisons of species abundances (Anderson et al. 2004). Studies involving estimates of relative abundance within antbird assemblages are necessary to test this hypothesis.

Because 100-ha scales are traditionally considered to be local samples of Neotropical forest bird diversity (Terborgh et al. 1990; Robinson et al. 2000; Blake, 2007), we expected that patterns of phylogenetic structure at this scale would resemble those of
the mixed-species flocks scale to a closer extent than those of the ecoregional assemblages. However, 100-ha plots consistently lacked phylogenetic structure at all the localities we analyzed (Fig. 2). Significant phenotypic structure was also lacking for all the traits analyzed at this scale (Fig. 3, Table 2). A plausible explanation for these patterns is that at 100-ha plots scale both competition and habitat filtering act in concert and mask each other's effects (see also Helmus et al. 2007). We did not analyze the phenotypic structure of macroecological traits at this scale because some of the variable we used vary over relatively coarse spatial scales, and because resolution of those that might vary within plots (e.g. elevation, aspect) was insufficient to finely characterize variation in traits among species within assemblages. It is possible that studies characterizing species niches based on abiotic variables at finer resolutions (see Loiselle et al. 2007) may be able to detect the effect of habitat filtering and competition.

Phylogenetic overdispersion in assemblages may arise as a result of competitive interactions, and because many studies assume phylogenetic niche conservatism, the most common explanation for phylogenetic overdispersion is that close relatives compete and exclude each other (Cardillo et al. 2008; Cooper et al. 2008; Bryant et al. 2008). However, if the assumption of phylogenetic niche conservatism is not met, one must consider alternative explanations for such pattern (Webb et al. 2002; Cavender-Bares et al. 2004), and this is the case in antbirds. Had we not tested for niche conservatism and assumed it to be true, we might have erroneously concluded that the coexistence of distant relatives in the regional assemblages is a result of competition (Webb et al. 2002; Cavender-Bares et al. 2004). However, our analyses reveal that convergent macroecological species' traits allow distantly related species to coexist at
regional scales and that phenotypic clustering is most likely a result of habitat filtering. This highlights the value of analyzing phylogenetic structure together with phenotypic structure and character evolution in order to better understand the processes involved in community assembly.

*Alternative explanations for patterns of phylogenetic structure*

As an alternative to the hypothesis of habitat filtering and convergent evolution leading to coexistence of distant relatives within ecoregional assemblages, phylogenetic overdispersion at this scale may arise as a consequence of the history of speciation of antbirds within Amazonia (see also Emerson & Gillespie 2008). Because allopatric speciation is the most common mode of speciation in birds (Barraclough & Vogler 2000), and because by definition areas of endemism are areas were there is a congruence of species’ distributional ranges as a result of a shared history of isolation and diversification, it is unlikely that closely related species (e.g. congeners) will co-occur within such areas simply as a result of biogeographic history. In other words, multiple distantly related clades with congruent distributions may contribute more species to regional assemblages than one or a few closely related clades, especially if members of particular clades have allopatric distributions as a result of purely historical reasons.

In addition, competition might be considered as a mechanism that can result in phylogenetic overdispersion at the ecoregions scale. Despite of the evidence suggesting habitat filtering at this scale, interspecific interactions have been proposed to limit species’ ranges by competitive exclusion between ecologically similar species. If closely related species are ecologically similar, then the fundamental niche is not
completely filled and the realized niche (sensu Pulliam 2000) is the reflection of past competitive interactions between closely related species, resulting in allopatric or parapatric distributions and hence phylogenetic overdispersion in ecoregions (Case et al. 2005).

Methodological Considerations

As described above, testing for niche conservatism can be particularly illuminating regarding the role of different processes of community assembly inferred from patterns of phylogenetic structure. Our analyses also highlight the importance of using two separate tests to evaluate trait evolution. Specifically, some studies have concluded that ecologically relevant traits are phylogenetically conserved simply based on randomization tests (e.g. Swenson et al. 2007). The fact that most of the traits we examined showed phylogenetic signal according to the randomization analyses but were more labile than expected under a Brownian motion model of evolution allowed us to interpret our results as a lack of phylogenetic niche conservatism. If only the randomization tests had been done, we would have erroneously concluded that antbirds do exhibit phylogenetic niche conservatism, which might have led us to reject the hypothesis that habitat filtering was predominant at the regional scale.

An additional consideration with respect to testing for phylogenetic niche conservatism is that some authors may argue that there is a radical difference between phylogenetic signal and phylogenetic niche conservatism (e.g. Losos 2008; Revell et al. 2008) and that the presence of the former is not an indicative of the latter. However, they all agree in that a lack of phylogenetic signal or a weaker signal than expected under Brownian
motion evolution would be enough to demonstrate that phylogenetic niche conservatism does not occur, which is specifically the case of the characters we studied in antbirds.

**Comparisons to Other Studies**

A recent study on wood warbler assemblages in North America showed that closely related taxa are less likely to co-occur, suggesting that present or past competitive interactions influence assemblages locally (Lovette & Hochachka, 2006). The contrast between these results and ours, which failed to reveal compelling evidence for competitive exclusion at local scales in antbirds, hints at the possibility that competition might be more relaxed in tropical settings, allowing close relatives to coexist at local scales. This provides one plausible explanation for the extremely high local diversity of birds in tropical forests. Certainly, more studies of this type are needed to evaluate whether this pattern can be generalized to other tropical and temperate taxa.

In addition to the warbler example noted above, phylogenetic overdispersion at local scales has been reported for a variety of assemblages (mostly of plants), where close relatives do not co-occur presumably due to competitive exclusion (Cavender-Bares et al. 2004; Cavender-Bares et al. 2006; Swenson et al. 2006; Swenson et al. 2007; Cardillo et al. 2008; Cooper et al. 2008; Bryant et al. 2008). In contrast, we are not aware of published evidence of phylogenetic clustering at local scales in plants or animals, which indicates that antbird assemblages may be unusual. Local bacterial assemblages along an elevation gradient are phylogenetically clustered at local scales (Bryant et al. 2008), but local scales may include enough habitat heterogeneity for microorganisms, which theoretically relaxes competition and increases the effect of habitat filtering.

**Conclusions**
The integration of ecology and evolutionary biology allowed us to make inferences about processes involved in community assembly that might account for diversity patterns in antbirds. Specifically, our findings support the hypothesis that habitat filtering is an important force structuring antbird assemblages at the regional scale. As localities within ecoregions share the same climatic variables, phenotypic clustering was expected. The lability of β traits in antbirds may be the mechanism that explains coexistence of distantly related species within the same ecoregion, providing new explanations to diversity patterns across Amazonia. However the biogeographical history of the clade and competition among closely related taxa may be alternative explanations to the pattern of phylogenetic overdispersion, our results are consistent with the habitat filtering hypothesis. Additionally, our results suggest that antbirds might not compete strongly for resources due to the low evidence of ecological differentiation and to the coexistence of close relatives within local assemblages. This provides a plausible explanation for the high local diversity of these birds in the Neotropics, highlighting the need for additional studies of this sort in order to better understand questions related to variation in diversity patterns. We suggest that such studies should take into account the evolution of traits in order to provide more accurate explanations to diversity patterns. However, more field information about specific traits that might be ecologically important and influenced by competition is needed to completely reject the competition at local scales hypothesis. Specifically, our study indicates (see also Losos 2008) that the assumption of phylogenetic niche conservatism has to be carefully considered, because it is clearly not general to all organisms.
References


Figure Legends

Figure 1
Map of the Neotropics showing the location of sites used to evaluate the phylogenetic structure of antbird assemblages. Black dots and their labels correspond to sites used to evaluate assemblages at the mixed-flock and 100-ha-plot scales. The areas colored in gray scale show the delimitation of ecoregions (Olson et al. 2001), sectors for which antbird distributions have been characterized (Isler 1997) are delimited with solid gray lines, and areas of endemism (Cracraft 1985) are delimited with solid black lines.

Figure 2
Indices of phylogenetic community structure and their 95% confidence intervals (NRI in black and NTI in gray) for each of the geographic scales evaluated, suggesting phylogenetic clustering at the understory mixed-species flocks level (left), essentially random assembly at the 100 ha plot level (center), and phylogenetic overdispersion according to the NTI and random dispersion according to the NRI at the ecoregion scale (right).

Figure 3
Trait evolution, measured in terms of the K statistic value in relation to the trait similarity within communities, measured as the number of randomizations that show smaller value than the observed value of Mantel correlation statistic. The vertical dashed lines indicate the two-tailed significance threshold for the Mantel test. Any points between both dashed lines indicate non-significant correlation values. The horizontal solid line indicates the threshold between trait lability and conservatism. Traits that fall above the line are considered conserved and those below are considered labile. The solid circles
and the grouping black solid line refer to the mixed-species flocks scale, the open circles and grouping dashed line to the 100-ha plots scale and the solid triangles in combination with the grouping solid gray lines to the ecoregions scale. Vocal, morphological and ecological traits treated as $\alpha$ traits do not suggest strong competitive interactions as they are distributed in all the quadrants and inside the threshold. Only one correlation suggests that phylogenetic clustering and significant phenotypic overdispersion are the result of competitive interactions acting over labile traits at highly local scales. The macroecological data suggest a strong influence of habitat filtering at regional scales as they fall into the bottom left quadrant of the plot. Such quadrant indicates that convergent traits in combination with clustering of traits forced by habitat filtering produce significant phylogenetic overdispersion.
Figures

Figure 1
Figure 3
Table Legends

Table 1
List of traits used to evaluate phenotypic structure of assemblages and trait evolution within the antbird family indicating to which factor (extracted from the PCA analysis) were correlated individual traits.

Table 2
Results of the Mantel tests between phylogenetic and phenotypic distance matrices used to evaluate the phenotypic structure of assemblages suggest phenotypic clustering for $\beta$ traits at the regional scale and generally non-significant phenotypic structure at the local and intermediate scales. * Significant Mantel correlation coefficients are highlighted with bold numbers. †PC indicates each of the factors obtained from the Principal Component analysis of the morphological, vocal and macroecological data sets. ‡F.S. refers to the foraging stratum trait assigned to the ecological data set.

Table 3
Results of the trait evolution analysis suggesting a general pattern of phylogenetic signal but evolutionary lability of ecological traits in the antbird family. PC indicates each of the factors obtained from the Principal Component analysis of the morphological, vocal and macroecological data sets. *F.S. is the foraging strata trait assigned to the ecological data set. †The words marked with asterisks indicate significant results for the test of phylogenetic signals.
### Table 1

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